Risk sensitive reproductive strategies

The effect of environmental unpredictability

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ABSTRACT

A crucial task in ecology is to quantify trade offs between competing demographic processes for experienced by individuals that inhabit unpredictable environments. Perhaps the most widely studied trade off is that between current reproduction and future survival ('the cost of reproduction'). While experimental studies have been widely used to quantify life history strategies in birds, virtually no experimental studies have been carried out on large and free ranging mammals. This thesis quantifies how female reindeer *Rangifer tarandus* subject to variability in food availability, trade their resources between reproduction and body mass to ensure own survival. By combining two experiments, one observational study and one theoretical model, this thesis show that: (1) Individuals subject to reduced food availability in one winter feeding promptly reduced their reproductive allocation the following summer to increased their autumn body mass. On the other hand, short-term improved conditions did not result in increased reproductive allocation. (2) Long-term improved winter feeding conditions did, however, result in increased reproductive allocation. (3) Reproduction was costly, especially for smaller females, as occasional harsh winters and high population density resulted in reduced reproduction and lowered female body mass. Moreover, a successfully reproducing female produced a smaller offspring in the coming year relative to a barren one. Reindeer also differ in their intrinsic quality as successfully reproducing females' showed an increased probability of reproducing also in the following year. (4) In harsh and unpredictable winter conditions, the optimal reproductive strategy involved a low reproductive allocation per unit female spring body mass. Under such conditions females increased their autumn body mass to enhance their own survival. Conversely, the optimal reproductive strategy in benign and predictable conditions involved a higher reproductive allocation. (5) Reproductive strategies and environmental conditions had significant effects on population dynamics. Female reindeer do not to jeopardize their own survival and adjust their reproductive allocation in order to buffer periods of low food availability in a risk sensitive manner.

Key words: cost of reproduction; evolution; environmental stochasticity; phenotypic plasticity; *Rangifer tarandus*; risk sensitive life histories.

PAPERS INCLUDED IN THE THESIS

Paper 1

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz and R. A. Ims. 2008. *Experimental evidence for a risk sensitive life history allocation in a long-lived mammal.* **Ecology** 89:829-837. (doi: 10.1890/07-0414.1)

Paper 2

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland and M. Nieminen. in press. *Experimental evidence of cost of lactation in a low risk environment for a long-lived mammal.* **Oikos**. (doi: 10.1111/j.1600-0706.2008.17414.x)

Paper 3

Bårdsen, B.-J., T. Tveraa, P. Fauchald and K. Langeland. manuscript. *Observational evidence of a risk sensitive reproductive allocation in a long-lived mammal.*

Paper 4

Bårdsen, B.-J., J.-A. Henden, P. Fauchald, T. Tveraa and A. Stien. manuscript. *Plastic reproductive allocation as a buffer against environmental unpredictability – linking life history and population dynamics to climate.*

PREFACE

INTRODUCTION

Biologists, anthropologists and psychologists have for a long time recognized that the theory of economic allocation of a limited budget can be useful in studies of optimal behaviour (e.g. Real and Caraco 1986, Stephens and Krebs 1986 ch. 6, Mace and Houston 1989, Mace 1990, 1993, Winterhalder et al. 1999). Risk sensitivity and related concepts have its roots within economical theory, but in biology risk sensitivity has its basis in studies of optimal foraging. The definition of risk used both in this thesis and its associated articles is similar to the definition used in risk sensitive foraging (reviewed in e.g. Real and Caraco 1986, Kacelnik and Bateson 1996): risk is defined as unpredictable variation in the outcome of behaviour, with consequences for an organism's fitness (the ultimate currency in evolutionary biology), utility (an economic currency) or value[1] (a synonym for both currencies: sensu Winterhalder et al. 1999, Winterhalder 2007). It is important to keep in mind that the probability distribution of outcomes can be known to the organism based on past experience, but stochasticity makes it impossible for organisms to predict with certainty any particular future outcome (Kacelnik and Bateson 1996). Risk is not the same as uncertainty, i.e. incomplete information, as risk cannot be overcome simply by acquiring more information (Kacelnik and Bateson 1996, Winterhalder et al. 1999, Winterhalder 2007). Risk sensitivity analysis is relevant for a wide range of different behaviours, such as reproductive behaviour (e.g. Bednekoff 1996, Winterhalder and Leslie 2002), as risk sensitivity should be presumed important whenever: (i) the fitness function is nonlinear, and (ii) one or more of the behavioural alternatives is characterized by unpredictable fitness outcomes (e.g. Stephens and Krebs 1986, Kacelnik and Bateson 1996, Winterhalder et al. 1999, Winterhalder 2007).

The fitness function (deduced from utility theory) makes an explicit assumption that organisms make consistent and rational choices based on the information they have at hand (Stephens and Krebs 1986). Specifically, organisms facing stochastic environments should solve two distinct problems: (i) the organisms must learn the fitness associated with different behaviours ('a problem of information'); (ii) then, the organism must select a strategy for exploiting those distributions ('a problem of risk') (Real and Caraco 1986). First, individuals that successfully track environmental fluctuations will have a selective advantage over poor trackers (Boyce and Daley 1980). Second, the relationship between reward[2] and fitness must be nonlinear if organisms are said to be risk sensitive (linear relationships imply risk neutrality: e.g. Stephens and Krebs 1986, Kuznar 2001, Kuznar 2002, Kuznar and Frederick 2003). If the fitness function is: (i) concave-down, i.e. negatively accelerating, individuals are said to be risk averse as the rate of increase in fitness decreases as the amount of reward increases ('the law of marginal diminishing returns'); and (ii) concave-up, i.e. positively accelerating, individuals are said to be risk prone as each unit of additions reward is valued more than the previous (Stephens and Krebs 1986: Fig. 6.1-2). Risk sensitivity can, thus, be used to understand under what circumstances individuals are willing to

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[1] 'Fitness' is used instead of 'utility' or 'value' through the rest of this study. Utility measures 'the level of satisfaction' associated with a specific good or decision (Kuznar 2001) and this is the basic organizing principle that individuals subject to certain constraints seek to maximize (e.g. Real and Caraco 1986). This can be illustrated using an example from economy: winning a price of 100 € makes a substantial contribution to the utility of a poor person, whereas the same prize makes an insignificant contribution to the utility of a multi-millionaire.

[2] 'Reward' can be used synonymously to 'wealth' or 'good', which is typically the same as 'individual state' (e.g. Houston and McNamara 1999).

accept or avoid gambling: being risk neutral[3] means that the cost of loosing is similar to the benefit of winning; being risk averse[3] means that the cost of loosing is large compared to the benefit of winning; whereas being risk prone[3] means the potential cost is minor relative to the benefit.

A central issue in life-history theory is how individuals allocate resources between current reproduction and future survival, a trade-off known as the cost of reproduction (e.g. Roff 1992, Stearns 1992). How environmental stochasticity affects life-history evolution is poorly understood except that long-lived organisms generally favor own survival over reproduction (e.g. Lindén and Møller 1989, Erikstad et al. 1998, Gaillard et al. 1998, Gaillard et al. 2000, Ellison 2003, Gaillard and Yoccoz 2003). Many organisms inhabit fluctuating environments, where fluctuations usually consist of a predictable seasonal component and a more unpredictable stochastic variation around this seasonal trend (**Paper 4**). Organisms inhabiting this type of environments have to make behavioural decisions without full knowledge about future environmental conditions (e.g. McNamara et al. 1995). Reproduction typically takes place during the favourable season (summer), whereas survival is particularly constrained in the unfavourable season (winter: Sæther 1997). In this type of environments, late winter conditions can have profound effects on both survival and reproduction (Coulson et al. 2000, Patterson and Messier 2000, Coulson et al. 2001, DelGiudice et al. 2002). Autumn body mass, which represents an insurance against winter starvation, is then traded against the resources a female can allocate to her offspring during summer as accumulation of fat reserves during summer might compete with lactation (Clutton-Brock et al. 1989, Clutton-Brock et al. 1996, Fauchald et al. 2004, Festa-Bianchet and Jorgenson 1998, Reimers 1972, Skogland 1985, Tveraa et al. 2003, **Paper 1**-**2**). Body mass is a proxy for condition or reserves, and an important trait affecting both survival and reproduction[4]. Consequently, in a given summer a female has to choose how many resources to allocate to somatic growth vs. reproduction: if a female allocates too much in reproduction this will reduce her ability to build an insurance against winter starvation (**Paper 1**-**4**).

Risk sensitivity in the context of the present thesis can be understood as a combination of the probability of encountering an extreme winter and the consequences such winters have on fitness (**Paper 1**-**4**). First, the outcome of a given reproductive allocation on survival is unpredictable due to the stochastic nature of winter climatic conditions (**Paper 4**): even though females might have 'estimated' this statistical distribution based on previous experience, environmental stochasticity makes any reliable forecasting of climatic events practically impossible[5]. Second, the relationship between winter weather conditions and fitness is nonlinear as: (i) the combination of an extremely harsh winter and low body reserves is not only fatal for reproductive success (e.g. juvenile and

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[3] In the 'standard design of risk sensitive foraging experiments' (reviewed by Stephens and Krebs 1986, Kacelnik and Bateson 1996) risk prone and risk averse have been defined as: "Given a choice between two equal means, an organism is said to be risk-prone if it prefers the more variable option and risk-averse if it prefers the less variable option" (Houston 1991). Conversely, an individual is risk neutral if it shows no preference.

[4] Body mass acts as a state variable (e.g. Houston and McNamara 1999), which is a currency that can be traded for reproduction or survival.

[5] Since meteorologists do only produce reliable predictions of weather phenomena for more than perhaps a few days into the future it is unlikely that wild herbivores can predict weather ~7 month into the future. Meteorologists have an advanced knowledge about weather systems (high level of information), but the stochastic nature of these systems makes accurate predictions far into the future impossible. The *Norwegian Meteorological Institute*, for example, does not forecast more than three months into the future (http://retro.met.no/sesongvarsler/introduksjon.html).

neonatal survival) but it can even greatly reduce adult survival (Skogland 1985, Clutton-Brock et al. 1992, Clutton-Brock et al. 1996, Aanes et al. 2000, Aanes et al. 2002, Tveraa et al. 2003); whereas (ii) extremely benign winters do not represent bonanzas as survival and reproduction are not boosted way above that of an average winter (Fauchald et al. 2004, **Paper 1-3**). Using terms from risk sensitivity, such an asymmetric response in the costs and benefits relative to environmental unpredictability indicates that long-lived organisms should be risk averse as they should be unwilling to expect the coming winter to be a benign one (**Paper 1**). It is important to keep in mind that organisms cannot manipulate the probability of encountering a harsh winter, but they can buffer the adverse consequences of such winters by reducing their summer reproductive allocation in order to increase their own autumn body reserves (Adams 2005, **Paper 1**). Organisms inhabiting such systems should not prepare for an average winter, but for extreme events that might happen from time to time (**Paper 2**).

The optimal reproductive strategy will, thus, depend on the expected winter environmental conditions. A changed distribution in winter conditions can have important consequences for both reproduction and survival. Individuals experiencing stable and benign winter conditions can afford a low autumn body mass and might therefore increase their reproductive allocation. On the other hand, animals experiencing harsh and variable winter conditions should maximize their autumn body mass by lowering their reproductive allocation. Accordingly, organisms experiencing unpredictable environments should adopt a *risk sensitive reproductive strategy* by adjusting their reproductive allocation during summer according to the chance of starvation the following winter (**Paper 1-4**). For a given body mass and distribution of environmental conditions, individuals can play different strategies (**Paper 4**). A *risk prone reproductive strategy* involves high reproductive allocation that will result in high reproductive reward during benign conditions, but high survival cost during harsh conditions. A low reproductive allocation will, on the other hand, result in high winter survival, but a low reproductive reward and represents a *risk averse reproductive strategy*. Moreover, when benign conditions appear for many years, individuals should increase their reproductive allocation as the amount of autumn body reserves that is needed for insurance against winter starvation will be lowered under such conditions. Population density, which in interaction with winter climate, can have profound negative effects on survival and reproduction (e.g. Grenfell et al. 1998, Coulson et al. 2000), are confounded with environmental conditions as harsh conditions generally supports lower densities than benign conditions (e.g. Morris and Doak 2002). Thus, density may also affect the optimal reproductive allocation strategy (**Paper 3-4**). For example, increased densities of reindeer *Rangifer tarandus* have direct effects on the individuals through increased competition for resources (Tveraa et al. 2007), and indirect effects through long-term effects on the pastures (Bråthen et al. 2007, Tveraa et al., *unpublished results*). In sum, environmental conditions and density have effects on how organisms should allocate resources between reproduction and somatic growth (**Paper 1-4**).

A *risk sensitive reproductive strategy* is one of several factors that can be of importance for population dynamics (**Paper 4**). Populations of large terrestrial mammalian herbivores (with an adult mass ≥ 10 kg: Gaillard et al. 2000 hereafter referred to as 'large herbivores') in northern and seasonal environments show different population dynamics. How individuals allocate resources into reproduction may provide an explanation for this. The Soay sheep *Ovis aries* on Hirta, Scotland

has, for example, a high population growth rate due to a high fecundity, low age at first reproduction and early lambing (Clutton-Brock et al. 1996, Clutton-Brock and Coulson 2002, Clutton-Brock and Pemberton 2004). Over-compensatory density dependence combined with harsh environmental conditions results in more or less regular events of mass starvation and population crashes during winter (Clutton-Brock et al. 1996, Grenfell et al. 1998, Coulson et al. 2001). In contrast, red deer *Cervus elaphus* on Isle of May, Scotland has a much lower population growth rate (Clutton-Brock et al. 1987). The population is regulated through a low fecundity, late age at maturity, late calving and direct density dependent juvenile mortality resulting in relatively stable populations (Clutton-Brock and Coulson 2002). In semi-domestic reindeer, Norway differences in productivity, due to differences in reproductive allocation as an adaptation to buffer winter climate severity (**Paper 1**-**3**), can have profound effects on population dynamics as: a combination of climate severity, harvest and foraging conditions has a profound impact on average population densities, individual body masses, and population dynamics (Tveraa et al. 2007). In sum, differences in reproductive strategies might have important consequences on the cost of reproduction and on population dynamics (Clutton-Brock et al. 1996, Clutton-Brock and Coulson 2002, **Paper 4**).

Apart from the assumptions underlying risk sensitivity, a few more assumptions should be fulfilled for defining *risk sensitive reproductive strategies*. First, organisms must be fitness maximizing, which is not an assumption specific for this study as it is a general assumption for evolutionary biology as a discipline (e.g. McNamara 2000, Coulson et al. 2006). Second, the organism of interest should be iteroparous (i.e. long-lived with many potential breeding attempts per lifetime: Schaffer 1974, Stearns 1992). This assures that an organism can spread the cost of breeding across several attempts. Third, the organism should experience unpredictable costs of reproduction. If no cost of reproduction does occur or if this cost is predictable there is no reason for spreading the potential negative consequences of reproduction over several breeding attempts. Fourth, the organism should be able to build energy reserves functioning as insurance against adverse environmental conditions. Fifth, the environment inhabited by the organism should be characterized by either strong seasonality (a favourable breeding season and an unfavourable non-breeding season) or at least by periods of favourable and unfavourable conditions. During the favourable season, organisms trade resources to reproduction against resources for building body reserves. The overall objective of this thesis was to investigate how environmental conditions affect reproductive strategies, and to investigate how interactions between optimal reproductive strategies and the environment can shape population dynamics. This thesis uses reindeer as a biological model as this species fulfils the above assumptions. The following research questions were addressed:

(1) How do improved and reduced winter feeding conditions on a short-term basis affect how individuals allocate their resources between reproduction and gain in body mass during summer (**Paper 1**-**3**)?

(2) How do long-term changed winter feeding conditions affect summer reproductive allocation (**Paper 1**-**2**)?

(3) How does the cost of reproduction vary according to individual quality, and factors extrinsic to the individuals like winter climatic conditions and population density (**Paper 1**-**4**)?

(4) How do winter climatic conditions affect the optimal reproductive strategy (**Paper 4**)?

(5) How do plastic life histories and climate affect population dynamics (**Paper 4**)?

METHODS

Study species and area

Reindeer belongs to the family Cervidae and the order Cetartiodactyla (Price et al. 2005). Cetartiodactyla is a relatively new order that includes the two former orders: Artiodactyla ('even-toed hoofed mammals') and Cetacea (whales & dolphins) (Price et al. 2005). Reindeer is a sexually dimorphic species where females are smaller than males (e.g. Reimers 1983, Reimers et al. 1983), and during most of the year the sexes are separated. The rut and conception happens in the autumn (e.g. Skogland 1994), and calving usually takes place in May (Reimers et al. 1983, Flydal and Reimers 2002). Reindeer are group living and highly migratory as they move between distinct summer and winter pastures (e.g. Folstad et al. 1991, Skogland 1994, Fauchald et al. 2007).

The thesis is based on empirical data from two semi-domesticated herds in Northern Norway (**Paper 1** & **Paper 3**) and one in Northern Finland (**Paper 2**). The number of semi-domestic reindeer in Norway increased towards the late 1980's (e.g. **Paper 3**:Fig. 1a). This trend was particularly strong in the northernmost part of Norway, where the peak in reindeer numbers was followed by a population decrease that continued throughout the 1990's (Tveraa et al. 2007: Fig. 1). The herds are organized in herding districts that are separated by fences and natural boarders. Since all animals are ear marked according to owner, virtually no effective movement between different populations exist (Tveraa et al. 2007). Our data source in Finland is from the research herd in Kaamanen, which consist of ~80 females with known life histories (**Paper 2**).

Scientific approach

Research on large herbivores has generally been performed using descriptive long-term observational studies and lack of experimental manipulations (Caughley 1981, Gaillard et al. 1998). Experiments on wild animals can be difficult to perform for practical reasons, especially for long-lived species that covers large geographical area, as experiments can be time consuming, expensive and impracticable (Turchin 1995). Consequently, there is still a need for long-term studies of marked individuals and with experimental designs that allow the relationship between population parameters and variables such as climate and density to be estimated (Festa-Bianchet et al. 1998, Gaillard et al. 1998). Semi-domestic reindeer provides a unique opportunity in this context because: (i) herds are gathered at least once each year for marking and slaughtering (e.g. **Paper 1** & **Paper 3**); (ii) they are managed within and exposed to the same natural environment as wild reindeer used a long time ago (Parks et al. 2002); (iii) it is easier to identify the mechanisms causing demographic changes in larger compared to smaller organisms (Sæther 1997); and (iv) it is possible, within a reasonable time frame, to generate knowledge of importance to researchers, authorities, as well as reindeer herders.

Ecological questions should be assessed with an analytical approach that combines statistical analyses of observational data, experiments, and mathematical models (Turchin 1995). The present thesis tests a common scientific hypothesis using these three approaches: an experimental protocol (**Paper 1** & **Paper 2**); an observational protocol (**Paper 3**); and a theoretical model (**Paper 4**). The

three approaches have different advantages and disadvantages. First, well-designed experiments[6] have an advantage compared to the other approaches as this type of studies can make so-called 'design-based inference', which is called 'strong inference' due to its ability to reveal evidence of causation (e.g. Quinn and Keogh 2002, Crawley 2003, Yoccoz and Ims 2008). A critical issue in ecological experiments, however, is whether the applied treatment is relevant for addressing the research question of interest and if the level of treatment is realistic with respect to a natural setting (discussed in **Paper 1** & **Paper 2**). Second, observational studies, which do not include the design properties of experiments, have the advantages of assessing research questions in a natural setting. This advantage, however, comes with the cost of possible confounding (discussed in **Paper 3**:S1). As observational protocols can only reveal 'model-based inference' they are often said to reveal 'weak inference' (e.g. Quinn and Keogh 2002, Crawley 2003, Yoccoz and Ims 2008). Third, models are useful tools in assessing mechanisms that might occur in nature. Numerous definitions exists of what models are and what they can be used for, but as there exist many different types of models developed for a wide range of different topics I will not enter such a general discussion. In the context of the present thesis it might, however, be useful to think of a model as an idealized, or simplified, representation of reality. These sorts of 'conceptual models' can be viewed as tools for testing arguments in a formal mathematical setting, where models can be used to test if specific patterns emerge from known processes and mechanisms given a set of more or less realistic assumptions (e.g. Kokko 2007).

Study design

Manipulation of winter conditions: supplementary feeding vs. natural pastures (**Paper 1**)

In both experiments in this study, which was performed in Northern Norway, females were included and allocated to different experimental groups according to the order in which they appeared in the corral. This was done under the assumption that this represented a sufficient randomization. We tested the design with respect to initial female body mass, a potentially confounding covariate (see *Introduction*), and as this state variable was equally distributed within the experimental groups we concluded that the study was sufficiently randomized. We used one herd where females had received supplementary feeding for years, and another herd where females utilized only natural pastures (see **Paper 1**:Fig. 1 for details). Manipulation of winter feeding conditions on a short-term basis was performed by moving individuals from one herd to the other: (i) translocation of individuals from the herd utilizing natural pastures to the herd receiving supplementary feeding ('improved winter conditions'); and (ii) translocation of individuals from the herd receiving supplementary feeding to the herd utilizing natural pastures ('reduced winter conditions'). Additionally, the control groups from the two experiments were used in an analysis of the effects of long-term supplementary feeding. Individual body mass as a response was recorded during summer, autumn and the coming winter. Multiple observations of females with a calf at foot were used to identify mother-calf relationships or whether a female was barren within a given year. The experiments were replicated in two different years (2003 & 2004) using a new set of individuals, and individuals were followed from January (initiation) to the next January (finalization).

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[6] The following assumptions are often discussed: manipulation (including controls), randomization, replication, realism and representation.

Manipulation of winter conditions and reproduction: supplementary feeding and reproduction (**Paper 2**)

This experiment was performed in Northern Finland during 2007-2008. Only initially pregnant females were included in this experiment, and a stratified-randomized design ensured that initial female body mass, and consequently also initial age, had the same distribution in the experimental groups (**Paper 2**). Individuals were assigned to one of two experimental manipulations: (i) environmental manipulation, which consisted of control females on natural pastures and a group of females receiving supplementary feeding; and (ii) reproductive manipulation, which consisted of control females that were lactating and a group where the offspring was removed 0-2 days after parturition (see **Paper 2**:Fig. 1 for details). Individual body mass, as a response, was recorded during winter, spring, summer, autumn, and the coming spring. Newborns were caught by hand and individually marked, and body mass, date of birth as well as offspring sex were also recorded. Individuals were followed from January (initiation) to April next year (finalization).

Increased population abundance and varying winter conditions: following two herds for six years (**Paper 3**)

This observational study was initiated by the marking of fifty prime-aged females (≥1 year) in each of two herds in Northern Norway. Both herds utilize the same winter pastures where they are kept together through the winter, but utilize different summer pastures. None of the herds were given supplementary feeding. The herds are separated on the winter pastures in the spring, and they are then herded to their respective summer pastures at the coast (**Paper 3**:Fig. 2). During the autumn migration, on the way back to the winter pastures, the two herds are again mixed and the annual migration cycle is ended. Individual body mass was recorded during spring and autumn, whereas calf production, mother-calf relationships and whether a female was barren or not were assessed similar as in the first study (**Paper 1**). Individuals were followed from April 2002 (initiation) to April 2008 (finalization). During this period population size increased dramatically.

Manipulating winter climate: changing the distribution of winter environmental conditions (**Paper 4**)

This simulation model, which is a follow-up to the previous empirical studies (e.g. **Paper 1-3**), used a state-dependent individual-based model (IBM) to investigate how females should optimize their reproductive investment in a stochastic environment that contains density dependent processes. The model excludes males as the aim was to assess female life-histories and because important parameters were widely available for females but not for males. Each time step was discrete (equalling one year) and divided in two distinct seasons: (i) summer where density dependent competition among individuals over a shared food resource occurred; and (ii) winter where temporal variability in environmental conditions affected individual survival and body mass losses. Individuals did not know the state of the coming winter conditions at the time when reproduction took place (summer). Winter environmental conditions were simulated assuming a normal distribution with three different average winter conditions ('control', 'improved' and 'reduced') and a gradient the distribution's standard deviation to mimic a gradient in environmental unpredictability.

RESULTS

Short-term changes in winter feeding conditions (Paper 1-2)

An asymmetric response to short-term improved vs. reduced winter conditions was present. When food availability was reduced, females immediately reduced their reproductive allocation the following summer (**Paper 1** & **Paper 2**), presumably in order to not compromise their own body mass at the onset of the next winter. On the contrary, when winter conditions were improved females were reluctant to increase their reproductive allocation (**Paper 1**). A small positive effect of short-term improved winter conditions was, however, found on offspring birth mass of initially smaller females in one study (**Paper 2**).

Long-term changed winter feeding conditions (Paper 1-3)

In contrast to short-term improved conditions, females that had been provided additional winter forage over several years allocated more in summer reproduction indicating that reindeer can track consistent changes in winter conditions (**Paper 1**). Moreover, winter feeding conditions for the Finnish herd, which has received supplementary feeding for years, were superior to most other Fennoscandian herds (**Paper 2**). This has probably resulted in an increased reproductive allocation by females in this herd as both reproductive success and offspring body masses were particularly high in this herd compared to the two other empirical studies (**Paper 1** & **Paper 3**). Female body mass was, however, also on average higher in the Finnish herd compared to the two Norwegian herds. This could be used as evidence against an increased reproductive allocation, but this might also indicate that these females have reached an upper threshold for which additional body mass does not translate into larger offspring or increased reproductive success. This can be explained by the fact that female reindeer are normally constrained to producing only one offspring per year so the consequence of allocating too many resources into reproduction during gestation can at best lead to giving birth to one very obese offspring.

The cost of reproduction and environmental conditions (Paper 1-4)

Winter conditions were unpredictable even though the degree of environmental stochasticity was varying across study areas (**Paper 2** vs. **Paper 1** & **Paper 3**); and extremely harsh and benign winters have asymmetric, or nonlinear, negative and positive consequences for the cost of reproduction (**Paper 2** & **Paper 4**). Lactating females gained less body mass during summer compared to barren ones (**Paper 2**-**3**). Additionally, this difference was negatively related to population density and winter climate indicating that a higher competition for resources had a more profound negative effect of reproducing compared to barren females (**Paper 3**). Moreover, successfully reproducing females allocated fewer resources into future reproduction by producing smaller offspring in the coming year (**Paper 3**). Individual quality was also of importance as: female body mass was a positive predictor of offspring body size within a period of ~9 months from birth (**Paper 1**-**3**); and successfully reproducing females experienced an enhanced probability of giving birth the next year (**Paper 3**).

Environmental conditions and optimal reproductive strategies (Paper 4)

The model (**Paper 4**), which synthesizes our understanding of the empirical results, showed that winter climatic conditions had a large effect on the amount of resources that reindeer should

allocate to reproduction vs. somatic growth during summer. This study generally confirmed the finding in the empirical studies (**Paper 1**-**3**). This study, however, also went a bit further as it showed that plastic reproductive strategies were superior compared to fixed strategies in all types of environments (**Paper 4**). For adults following a plastic strategy, reproductive allocation was estimated and updated each year according to the individuals' spring body mass. This ensured that females in poor body condition during spring either skipped reproduction or reduced their reproductive allocation in order to enhance their body reserves during summer. A fixed strategy, on the other hand, implied that females always allocated a constant proportion of its spring body mass to reproduction (**Paper 4**:A1). This severely limited females following this strategy from buffering periods of reduced forage availability.

Plastic strategies with a low reproductive allocation per unit female spring body mass did win in the most unpredictable environments (**Paper 4**:Fig. 3). This relationship was, however, weakest for improved environmental average. Similarly, strategies involving a higher reproductive allocation per unit spring body mass did win in more predictable environments for all environmental averages except for the improved one. The latter was more an effect of population density, which was confounded with environmental conditions (**Paper 4**:Fig. 5). Moreover, the realized average reproductive allocation interacted with environmental average and stochasticity, and average population density: the lowest reproductive allocation was found in harsh and unpredictable winter conditions and during high density (**Paper 4**:Fig. 4).

Environmental conditions, reproductive allocation and population dynamics (Paper 4)

Populations inhabiting benign and predictable winter conditions were most sensitive to climatic perturbation. These populations supported the highest population densities, which in interaction with climate limited the possibility for individuals to buffer adverse climatic effects. Negative density dependence had a strong negative effect on offspring body mass and consequently on reproductive success: the combination of high density, which resulted in lowered offspring autumn body mass, and an extremely harsh winter had dramatic negative effects on offspring survival. A high reproductive allocation also resulted in lowered female autumn body mass in these good environments, which gave the potential for very low adult survival rates in the rare occasions of an extremely harsh winter.

Populations subject to poor winter conditions were, on the other hand, characterized by low density, and these populations were least sensitive to climate. A low reproductive allocation resulted in increased female autumn body mass, and a consequently high adult survival in these environments. This model did not include any predation or harvest, but harsh winters apparently 'harvested' these populations by removing especially younger individuals. This released these populations from negative density dependence, and this had a positive effect on reproduction as females received a higher reproductive reward (for a given allocation value) during low compared to high density (**Paper 4**:A1).

DISCUSSION

Female reindeer, which are long-lived with many potential breeding attempts during a lifespan, do not want to jeopardize their own survival over reproduction. Consequently, females have adopted a *risk sensitive reproductive strategy* where they trade reproduction against the amount of autumn body reserves needed for survival insurance during the coming winter (**Paper 1-4**). Being risk sensitive implies that individuals to some degree are either risk prone or risk averse, where female reindeer are risk averse because: (i) during the summer they cannot predict with certainty the coming winter; and (ii) extremely harsh and benign winters have asymmetric fitness consequences (mainly through their effects on adult survival). Female reindeer are, thus, not willing to gamble that a coming winter will be a benign one, because the cost of preparing for a benign winter but meeting a harsh one is dramatically higher than the benefit of preparing for a benign winter and actually get one. Consequently, female reindeer optimized their allocation in reproduction vs. somatic growth according to expected winter conditions, but individuals do not prepare for an average winter, but for extreme winters (relative to past experience) that might happen from time to time. Such effects of environmental conditions on life histories have important consequences for both individual survival and reproduction, and hence also on population dynamics.

Many of the assumptions for a risk sensitive reproductive investment are, at least partly, fulfilled for many long-lived organisms as they experience a temporally varying cost of reproduction, they build body reserves during periods of favourable environmental conditions and they use these reserves as a buffer against unpredictable environmental variability during periods of non-favourable conditions [e.g. humans (Bronson 1995, Lummaa and Clutton-Brock 2002), large herbivores (Sæther 1997, Gaillard and Yoccoz 2003), birds (Lindén and Møller 1989, Parker and Holm 1990, Hanssen et al. 2005), fish (van den Berghe 1992, Hutchings 1994, Klemetsen et al. 2003) and reptiles (Shine 2005, Radder 2006)].

The ability for individual's to buffer negative climatic effects by adopting a *risk averse reproductive strategy* has important consequences for how the impacts of future climate change will be. These changes will most likely result in a shift towards more frequent extreme precipitation events (e.g. Wilby and Wigley 2002, Semmler and Jacob 2004, Tebaldi et al. 2006, Benestad 2007, Sun et al. 2007). Moreover, many of these climatic scenarios are expected to happen both sooner and more pronounced in the northern hemisphere (e.g. Tebaldi et al. 2006, Benestad 2007), which is why current efforts to understand the impacts of future climate change should focus on these systems. Hanssen-Bauer et al. (2005), for example, review several studies predicting how future climate change will affect Fennoscandia. The most important finding of this, and other studies, is a predicted shift between warm and cold periods during winter coupled with a year-round increased intensity of precipitation. Such shifts will lead to an increased frequency of wet weather, deep snow and ice crust formation that has negative consequences for large herbivores (e.g. Solberg et al. 2001).

Many recent analyses of climatic effect signatures in population time series have been used to infer the likely consequences of future climate change (Stenseth et al. 2002). The impact of future climate change commonly invokes more frequent population collapses (e.g. Post 2005). Such

inferences are based on an underlying assumption that animals have non-plastic life history strategies that are not adequately adaptive to new climate regimes. The studies in the present thesis, however, suggest that these changes will more likely result in a change towards more risk averse life histories that have the potential of buffering negative effects of climate up to a certain point where extinction is inevitable. I, thus, propose that future studies should focus more on how long-lived organisms may adjust their life histories to counteract climate changes.

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PAPER 1

Experimental evidence for a risk sensitive life history allocation in a long-lived mammal

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz

& R. A. Ims

PAPER 2

Experimental evidence of costs of lactation

in a low risk environment for a long-

lived mammal

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland & M. Nieminen

PAPER 3

Observational evidence of a risk sensitive reproductive allocation in a long-lived mammal

Bårdsen, B.-J., T. Tveraa, P. Fauchald & K. Langeland

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PAPER 4

Plastic reproductive allocation as a buffer against environmental unpredictability – linking life history and population dynamics to climate

Bårdsen, B.-J., J.-A. Henden, P. Fauchald, T. Tveraa & A. Stien

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